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Conservation network design for endemic cacti under taxonomic uncertainty

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ABSTRACT

The utility of spatial conservation prioritization (SCP), could be limited by the biases produced by taxonomic uncertainty and by the lack of an accepted taxonomic checklist for a diverse group of species. Using information on the endemic cacti of the Atacama Desert and Mediterranean Chile, we assessed the implications for SCP of the existence of two contrasting taxonomies. Biological and socioeconomic criteria were combined to design conservation networks for two widely used taxonomic checklists of endemic Chilean cacti. We analyzed the spatial distribution of these conservation networks to assess the congruence of the taxonomic checklists and evaluated whether our models match the geographic distribution of the National System of Protected Areas. The conservation networks had low similarity. However, consensus scenarios revealed several coincident priority sites. Gap analyses indicated that one-third of the species were completely unprotected but that all species were satisfactorily protected in the consensus scenario. Consensus scenarios based on different checklists can improve SCP because this approach is less affected by taxonomic uncertainty. It is more conservative (without a priori taxonomic decisions) and robust (priority sites are supported by more than one scenario). Given the narrow distribution of cacti, effective conservation actions demand environmental actions in a geographically explicit framework.

1. Introduction

In the face of current rates of biodiversity extinction, the spatial design of conservation networks requires the integration of complex biological and socioeconomic criteria (Sanderson et al., 2002). Spatial conservation prioritization (SCP) is a modeling process for identifying priority areas for conservation (Margules and Pressey, 2000; Wilson et al., 2005) where both biological (Vane-Wright et al., 1991) and socioeconomic variables (Sanderson et al., 2002; Naidoo et al., 2006) are explicitly and quantitatively incorporated into the conservation network design (Possingham et al., 2000; Margules and Pressey, 2000; Williams and Araujo, 2002; Pressey et al., 2007; Carwardine et al., 2008). These strategies are based on a growing body of evidence that drivers of the loss of biodiversity (habitat loss, biological invasions, land-use change) are strongly correlated with socioeconomic growth (Brooks et al., 2002; Giam et al., 2010).

A crucial aspect in SCP is the application of multiple biological criteria because different aspects of species are involved in their conservation values (e.g., phylogenetic uniqueness) and their vulnerability to extinction (e.g., threatened status of species) (Vane-Wright et al., 1991; May, 1990; Myers, 1988; Cadotte and Davies, 2010; Moilanen et al., 2009). Taxonomic uncertainty in many biological groups can challenge SCP because inflated species numbers could generate network designs that excluded certain species, whereas other species would be overrepresented (Isaac et al., 2004; Mace, 2004). Among the biological criteria that are used for SCP, the evolutionary history of species has been widely recognized as a relevant characteristic that should be incorporated into conservation (May, 1990; Vane-Wright et al., 1991; Cadotte and Davies, 2010; Winter et al., 2013). The principal evolutionary proxy used to assess the relative importance of taxa is phylogenetic distinctiveness, namely, the unique proportion of a phylogenetic tree that a species represents (Tucker et al., 2012). The principle that guides conservation practice based on phylogenetic distinctiveness is that extinction from a species-rich clade will result in a smaller loss of evolutionary information than extinction of a highly distinct species from a species-poor clade (Winter et al., 2013). Additionally, taxonomic checklists do not always reflect







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current knowledge of the phylogenetic relationships within clades; thus, the incorporation of criteria related to phylogenetic distinctiveness may improve conservation actions (Isaac et al., 2004; Morrison et al., 2009). Finally, the inclusion of the threatened status of species as a biological criterion in SCP is desirable because species statuses are often based on quantitative measures of extinction risk (Lamoreux et al., 2003). However, the use of red lists in SCP must be complemented with additional biological criteria because conservation efforts will otherwise be biased toward protecting only endangered species (Possingham et al., 2002).

Explicit biological criteria are the key to spatial conservation, but it is necessary to incorporate socioeconomic variables to achieve conservation goals more efficiently (Naidoo et al., 2006). In this sense, one of the advantages of SCP is to achieve the stated goals at the lowest cost. The heterogeneity of costs in geographic space can be considered in terms of the 'human footprint' (Sanderson et al., 2002). According to this concept, a strong human influence can result in high costs for conservation.

The Cactaceae, with more than 1600 recognized species, is one of the most conspicuous and diverse Angiosperm families in the Neotropics (Anderson and Brown, 2001). In addition to the large number of species, a remarkable characteristic of the group is the predominance of narrow endemism (Hernández and Bárcenas, 1995, 1996; Mourelle and Ezcurra, 1997; Guerrero et al., 2011a). In the Chilean flora, Cactaceae is a diverse family that requires urgent conservation action because it has elevated levels of endemism in the country (>90%) and most species are threatened by human activities (Marticorena, 1990; Hoffmann and Walter, 2004; Larridon et al., 2014). Cacti are a dominant floristic element that determines the phytogeography and vegetation structure of the Atacama Desert and Mediterranean Chile (Armesto et al., 1979; Rundel et al., 1991), and they are a crucial group for the world hotspot defined as Chilean winter rainfall-Valdivian forest (Arroyo et al., 1999, 2004). The geographical distribution of Chilean endemic cacti is between 18° and 36°S, with the highest species richness concentrated at lower elevations (<1000 m.a.s.l.) and middle latitudes (between 25° and 28°S) (Hunt, 2006; Guerrero et al., 2011a, 2011b). Unfortunately, Chilean cacti have a uncertain taxonomy, and these taxa have undergone nomenclatural changes with no consensus on a unique taxonomic checklist (Kattermann, 1994, 2001; Hunt, 2006; Zuloaga et al., 2008). Although the distribution of cacti has been amply documented (Graham, 1998; Hunt, 2006; Guerrero et al., 2011a,b), the lack of uniformity in the taxonomy employed detracts from the efficiency of conservation actions.

Our study aimed to design conservation networks for the endemic cacti of the Atacama Desert and Mediterranean Chile using SCP based on several biological criteria (phylogenetic distinctiveness, threatened status and distribution range) and incorporating a socioeconomic factor, the 'human footprint' (Sanderson et al., 2002). Based on the criteria listed above, we built conservation networks for two different taxonomic checklists (scenario 1 and 2). We characterized and analyzed the spatial distribution of these conservation networks to evaluate the impact of the use of different taxonomic checklists in SCP. Additionally, because many protected areas around the world have been deficient in protecting threatened species (Bunin and Jamieson, 1995; Contreras-Medina et al., 2010), we evaluated the representation of all endemic cacti in the Chilean National System of Protected Areas (hereafter, NSPA) and in our conservation networks.

2. Methods

2.1. Study area

Our study focused on the Atacama Desert and Mediterranean central Chile between 18°S and 36°S, ranging from sea level to

4000 m altitude. These areas are distinguished by not only high levels of endemism in their flora and fauna but also a high rate of landscape modification and are considered a global biodiversity hotspot priority for conservation (Myers et al., 2000). Atacama Desert and Mediterranean central Chile configure an arid gradient where arid adapted lineages have diversified (Guerrero et al., 2013; Jara-Arancio et al., 2014), and harbors all of the diversity of Chilean endemic cacti, including notable examples of species with extremely restricted geographic ranges (Ortega-Baes and Godinez-Alvarez, 2006). We decided to work with endemic cacti because other non-endemic species are distributed in border areas but occur only sparsely in Chile, in contrast to their geographic representation in neighboring countries.

2.2. Conservation features: species checklists, occurrence database and species distribution modeling

We used two taxonomic classifications currently used in scientific studies and government conservation planning (MINSEGPRES, 2007 to 2011; Squeo and Gutiérrez, 2008). Checklist 1 (CL1) was first published by Hunt (2006) and later modified by Hoffman and Walter (2004) and by Guerrero et al. (2011a); this checklist includes 73 species and 8 genera. Checklist 2 (CL2) was employed by Zuloaga et al. (2008) and includes 78 species and 12 genera. The proportion of agreement between the two checklists is 0.43, the nomenclature used and the correspondence between the two checklists are shown in Table S1 in Supporting Information.

To infer species distributions, we made species distribution models (SDMs, Elith et al., 2011) based on a maximum-entropy algorithm that estimates the suitability of the habitat of a group of georeferenced occurrence localities for the species (Phillips et al., 2006). The occurrences were obtained from field research (2005-2011; see details in Guerrero et al., 2011a) and from specimen records from two national herbaria (CONC and SGO). The number of occurrences per species is given in Table 1, Supporting Information. Species distribution models were constructed using MaxEnt v. 3.3.3 (Phillips et al., 2006) and incorporated the 19 climatic variables available in Worldclim (Hijmans et al., 2005). We obtained 10 replicates (with a bootstrap adjustment based on 500 iterations) for each species, and we used the averaged predicted distribution. For best model performance, we selected the regularization multiplier $\beta = 1$ to avoid overfitting the data. We used 10,000 pseudo-absence random points because predictive accuracy is higher (Phillips and Dudik, 2008; Barbet-Massin et al., 2012). We set the random test percentage to 25% for evaluating the accuracy of each model and calculated AUC areas using MaxEnt. The output was classified as zero (absence) or one (presence). The threshold was set in accordance with the fixed sensitivity method (Pearson and Dawson, 2004), meaning that 90% of the occurrence localities used in calibration will be included in the prediction. For species with fewer than five occurrences, we did not use distribution models but only included georeferenced occurrences.

2.3. Conservation network design

To define priority areas for conservation, we generated a georeferenced system of planning units and assessed the relative conservation value of each one; the value of the planning units was obtained by reaching a particular biodiversity representation based on several attributes of areas (both biological and economical) penalized by the breaching of any of several criteria ('cost' of the reserve system, Ball et al., 2009). The spatial modeling that optimized priority site selection was conducted with the simulated annealing algorithm, which minimized the 'costs' of the reserve system while simultaneously reaching an optimal biodiversity representation (Ball et al., 2009). This modeling was performed with Marxan 2.43 (Ball et al., 2009). In this study, we constructed a grid made up of 6576 hexagonal planning units, each with an area of 100 km². All georeferenced data were processed using ArcGIS 9.3 (ESRI, USA).

Two conservation network scenarios were modeled: scenario 1 and 2, based on checklist 1 and 2, respectively. For each scenario, we incorporated three biological criteria per species to define the parameters of the network model: predicted distribution, threatened status and phylogenetic distinctiveness. The specifications for each criterion and the parameters are detailed in Section 2.4. Complementary socio-economic variables were included in our models using the 'human footprint' (Sanderson et al., 2002) (detailed in Section 2.5) in the planning unit cost file. As a measure of the spatial connection among planning units, Marxan is based on a definition of a boundary length modifier (BLM). In each scenario, we configured the BLM (Figs. 1 and 2, Supporting Information) to determine the most efficient value (Stewart and Possingham, 2005). Following to Game and Grantham (2008) to set the status of the planning unit, "0" was used for units that belong to areas without current protection and "2" for units that are currently protected by the National System of Protected Areas.

We ran Marxan 10,000 times for each scenario and selected 10,000,000 iterations for each. Also, for each scenario we generate frequency selection, i.e. between 10,000 runs for each scenario, the number of times any one of the selected planning units, and best scenarios, i.e. between 10,000 runs for each scenario, the scenario that best represents the conservation features. We analyzed the congruence between frequency selection scenarios, calculating Pearson correlations using SPSS v21.0.0 (IBM SPSS Statistics, 2013). We also tested the congruence between best scenarios, calculating Cohen's kappa coefficient with the psy package in R (R Development Core Team, 2009). Additionally, we generated consensus networks based on the best models from scenario 1 and 2. The consensus network based on the best solution scenarios was constructed by choosing planning units that were shared by the best models from scenario 1 and 2.

2.4. Conservation features and biological criteria

We used three biological criteria for conservation network design: the conservation status of species (to define the species penalty factor – SPF), the area of occupancy (to define a feature representation target for each conservation feature) and phylogenetic distinctiveness (to define a target for feature occurrence).

The features penalty factor in Marxan (also species penalty factor – SPF) is a multiplier that sets the value of the penalty that will be added to the objective function if the target for a conservation feature is not met in the reserve selection (Game and Grantham, 2008). This value was determined by the level of threat faced by the species. In particular, we used the official red list based on the National Process of Classification of Threatened Species (MINSEGPRES, 2007 – 2011), but because this process is still in progress (40% of the endemic species have been classified), we complemented the information about threatened species with other conservation assessments (Hoffmann and Walter, 2004). Since the threat level can change with changes in taxonomic identity, we used appropriate threat status in coherence of species checklists. Threatened species have a high SPF value, and species of least concern have a low SPF value. To calibrate SPF, a sensitivity analysis was performed with Zonae Cogito software (Segan et al., 2011).

The feature representation target for each species is defined by the area of occupancy. Here we established the target thresholds at 100 per cent of the distribution of each species with an area of occupancy of less than 500 km², 20 per cent of the distribution of each species with an area of occupancy of greater than 125,000 km² and 20–100 per cent of the distribution of each species with an intermediate area of occupancy (interpolated) (Rodrigues et al., 2004; Wilson et al., 2005).

The target for feature occurrence in Marxan is the minimum number of planned conservation units or conservation features (occurrence) required in a reserve system (Game and Grantham, 2008). This value was defined by the phylogenetic distinctiveness estimated using the w-May index, which counts the number of branches descending from each node that lies on the path from a species tip to the root in a phylogeny (May, 1990). To obtain the w-May index, we assembled a meta-tree hypothesis for Chilean endemic cacti; this meta-tree was constructed to generate a topology of Chilean endemic cacti following the Cactaceae phylogenies published elsewhere (Nyffeler, 2002; Griffith and Porter, 2009; Nyffeler and Eggli, 2010: Bárcenas et al., 2011: Guerrero et al., 2011b). The polytomies of the meta-tree were solved to the lowest taxonomic level possible depending on the available phylogenetic information; the meta-tree was drawn manually using Mesquite 2.74 (Maddison and Maddison, 2010). The resulting topology was age-calibrated based on the divergence times of cacti reported by (Wikström et al., 2001) using the branch-length adjuster algorithm implemented in PHYLOCOM (Webb et al., 2008). The resulting phylogeny shows 126 terminal tips and 39 internal nodes (Fig. 1); this phylogeny was used to obtain the w-May index by applying the tax. Distinctiveness function available for the Picante package (Kembel et al., 2010) in R 2.14.0 (R Development Core Team, 2009). The w-May index was converted into a percentage ranging between 0% and 100% of the distribution of the species and this percentage is defined as the target for feature occurrence in Marxan. For this purpose, the index (values between 0 and 1) was then transformed to a rescaled percentage by multiplying by 100.

2.5. Socioeconomic criterion

To incorporate a socioeconomic criterion into our model, we included the 'human footprint', a variable that measures the human influence on the surface of the earth (Sanderson et al., 2002). This variable was represented by a map of the human influence, represented by an index calculated from four variables: human population density, land transformation, human access and power infrastructure. We included the human footprint as a value of conservation cost for each planning unit, with a minimum



Fig. 1. Meta-tree depicting the phylogenetic relationships among Chilean endemic cacti. The tree was constructed with the grafting method (see text for details). Identities of studied clades are marked and colored along the semicircles around the tree, and these identities are labeled according to their presence in checklist 1 or checklist 2. (A) *Eriosyce s.l.*, (B) *Echinopsis + Haageocereus*, (C) *Eulychnia + Austrocactus*, (D) *Copiapoa*, (E) *Maihueniopsis + Miqueliopuntia*, (F) *Pyrrhocactus*, (G) *Telocephala*, (H) *Neoporteria*, (I) *Eriosyce s.s.*, (J) *Islaya*, (K) *Trichocereus + Haageocereus*, (L) *Maihueniopsis + Austroclindropuntia*. Scale bar represents 5 million years.

value of 0 (low human footprint and low cost of conservation) and a maximum value of 100 (for high human footprint and high cost of conservation). We ran a sensitivity analysis by visual inspection and set the footprint value between 0 and 100, with the same values of the human footprint.

2.6. Gap analysis

The NSPA in Chile selectively covers large areas of the southern Chile regions, leaving entire ecosystems in northern and central Chile underrepresented (Luebert and Becerra, 1998; Rodrigues et al., 2000). Historically, the goals of this network have been defined to protect charismatic endangered species (e.g., Reserva Nacional Las Chinchillas, implemented to conserve the mammal Chinchilla lanigera) and scenic landscapes or natural resources of strategic importance (e.g., Campos de Hielo Sur, implemented to conserve southern ice fields). We analyzed the representation of endemic cactus species for checklist 1 and 2 in the NSPA by overlapping layers of the predicted species distributions with the official layer of NSPA. We identified three categories of representation: gap (0% of cacti distribution protected), partial gap (1-99% of cacti distribution protected) and protected (100% of cacti distribution protected). These analyses were performed on ArcGIS 9.3 (ESRI, USA). We also performed two independent analyses to compare the levels of representation of each species in the NSPA and in the consensus network based on the best models. Specifically, we overlaid the distribution models of cacti species with the layer of the NSPA and with the best model consensus scenario. To assess gap, we considered that species whose distributions covered <500 km² should be completely under protection (Rodrigues et al., 2004), whereas species with wide distributions (>125,000 km²) should be protected in at least 20% of their distribution range (Rodrigues et al., 2004).

3. Results

3.1. Conservation network design

Modeling scenarios 1 and 2 revealed a similar pattern for the frequency distribution of selected planning units ($r^2 = 0.93$, P < 0.005; Fig. 2a and b). The best solution of scenario 1 recovered a total of 2 315 planning units (35.2% of the total); these areas were

located primarily in coastal areas of northern and central Chile (Fig. 2). The best solution in scenario 2 recovered a similar sized area with 1969 planning units (29.9%) and was located primarily in coastal areas in central Chile and generally in inland areas in the north. The selected best models of scenarios 1 and 2 followed different spatial patterns, as indicated by the low Cohen's kappa (-0.01). The consensus scenario based on the best models recovered 2 426 planning units (36.9% of all planning units); the planning units for this consensus were located primarily in coastal and inland areas in northern and central Chile.

3.2. Gap analysis and conservation targets

Among the total number of endemic species of cacti in Chile, 23 species (29.5%) and 19 species (27.1%) on checklists 1 and 2, respectively, are completely unprotected by the NSPA (Fig. 3). Most species are protected only in small areas (partial gap). This includes 55 species on checklist 1 (70.5%) and 51 species on checklist 2 (72.9%; Fig. 3). Additionally, the relationship between the size of the distribution range of the species and the species representation targets indicated that the NSPA is deficient in protecting the diversity of endemic cacti for both CL1 and CL2 (Fig. 4). In contrast, the consensus scenario covered >40% of the species representation targets for CL1 and CL2 (Fig. 4).

4. Discussion

The endemic cacti of northern and central Chile include several taxa distributed in the Atacama Desert and Mediterranean areas. The lack of exhaustive phylogenetic studies and the different splitter–lumper taxonomic cultures challenge spatial conservation planning. This situation is not only problematic for cacti because biologists have been faced with the difficult task of defining and delimiting valid species; it commonly occurs that a species is assigned to different taxonomic ranks (specific or intraspecific; Mallet, 2008). If species are closely related in phylogenetic terms and belong to a diverse group, the difficulty of taxonomic issues increases. In turn, this situation may commonly produce more than one taxonomic ordination or result in inconsistencies in species lists (Brown, 1959; Fitzpatrick and Turelli, 2006). Our approach based on consensus scenarios can be employed in other biological groups with taxonomic uncertainty and has the advantage of being



Fig. 2. Geographical distribution of the best planning units and selection frequency for each for two scenarios based on two taxonomic checklists. Biological and socioeconomic criteria were combined to design conservation networks. Best scenario for checklist 1 (a) and its selection frequency (b); best scenario for checklist 2 (c) and its selection frequency (d). In (e), consensus scenario.



Fig. 3. Gap and partial gap analysis for checklist 1 (a) and checklist 2 (b).

taxonomically explicit and conservative because it involves no preference for any taxonomic checklist. Accordingly, these consensus scenarios are less strongly affected by the intrinsic biases caused by taxonomic uncertainty.

The importance of using different taxonomies to construct a consensus conservation network is critical. Although we detected a correlation between the frequency distributions of the units selected under the two scenarios, the comparison between best models strongly suggests that taxonomic uncertainty can indeed impact the solution of an SCP (Cohen's kappa = -0.01; Fig. 2). Therefore, the utilization of a single checklist can have profound consequences in species conservation, as certain species can be completely unrepresented in conservation networks. This situation requires the development of new approaches and tools that can reinforce conservation actions. The utilization of consensus networks can produce more robust results than relying on a single checklist because a consensus should be less affected by taxonomic biases, simply because the coincidences between individual models can support the selection of numerous priority sites. Indeed. an important coincident priority site for endemic cacti is the almost continuous coastal area in the Atacama Desert between the coastal localities of Paposo (25°01'S) and Coquimbo (30°5'S) (Guerrero et al., 2011a). This long area, known as the 'blooming desert', is recognized as a priority area for conservation of vascular plants due to its high diversity and concentration of endemism (Cavieres et al., 2002; Squeo and Gutiérrez, 2008). Despite the high conservation value of the blooming desert, the area is threatened due to extensive desertification (Groh, 2007) and the intensive impact of economic activities such as rally raid competitions, thermoelectric industries, agro-industrial companies and metal mining industries. The narrow distributions of several Chilean cacti have placed them at risk in the face of global changes that are pushing endemic species to an irreversible extinction threshold (Rodrigues et al., 2004).

The gap analyses revealed poor species protection by NSPA. Currently, one-third are not protected, two-thirds are partially protected and no species is fully protected (Fig. 3). Additionally, the relationship between the size of the distribution range of a species and the species representation target reinforces the idea of limited species representation in NSPA for species included either in checklist 1 or in checklist 2. In contrast, no gaps where retrieved when analyzing our consensus network. Our results are consistent with other studies that show how the biased distribution of NSPA



Fig. 4. Relationship between the size of the distribution range of a species and the percentage of the range that is protected (species representation target) by the National System of Protected Areas (gray circles) and by our proposed consensus networks for Checklist 1 (white circles) and Checklist 2 (black triangles). Note that symbols can overlap because different checklists can use the same taxa but with different species or genus names.

negatively impacts the adequate protection of terrestrial vertebrates and even entire ecosystems (Luebert and Becerra, 1998; Tognelli et al., 2008). In our consensus conservation network, species had more than 40% of their distribution protected; to achieve this percentage, 192,706 km² should be allocated to in situ conservation. This finding is less encouraging because current national protected areas in Chile only cover 14,533 km² (3.12%) of the Atacama Desert and Mediterranean areas. Therefore, the NSPA should increase its spatial coverage to achieve satisfactory levels of species representation. The substantial area required for the optimal conservation of Chilean endemic cacti should encourage environmental authorities to adopt additional and complementary conservation actions that must extend beyond the establishment of national protected areas. Indeed, accurate and exhaustive territorial planning should be encouraged to define and quantify threats with a spatial basis. We hope that our study can contribute to highlight the relevance of taxonomic studies in conservation and also provide relevant information that will be used in the design of priority sites, and support the creation of new environmental policies with a geographically explicit framework.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.05. 028.

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